A network linking perception and memory systems in posterior cerebral cortex.

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ABSTRACT

Here, we report a new network of brain areas bridging the spatial-memory and scene-perception systems of the human brain. Using fine-grained individual-subject fMRI, we reveal three cortical areas of the human brain, each lying immediately anterior to a region of the scene perception network in posterior cerebral cortex, that selectively activate when recalling familiar places. Despite their close proximity to the scene-perception areas, network analyses show that these regions constitute a distinct functional network that interfaces with memory systems during naturalistic scene understanding. This new network, which conveys memory signals to visually-responsive posterior cortex, offers a new framework for understanding how the brain implements memory-guided visual behaviors like navigation.

MAIN TEXT

As we navigate through our visual world, the scene in front of us is seamlessly integrated with our memory of the broader spatial environment. The neural systems supporting visual scene processing in posterior cerebral cortex[1–7] and spatial memory in the hippocampus and medial temporal lobe[8–16] are well-described. But how do visual and spatio-mnemonic systems interface in the brain to give rise to memory-guided visual experience?

Two disparate lines of inquiry yield different hypotheses. On the one hand, mechanistic accounts of perceptual memory often posit that explicit recall of visual stimuli reinstates perceptual representations in visual areas, including the three areas of the scene-perception network (parahippocampal place area (PPA), occipital place area (OPA), and medial place area (MPA))[17–20]. However, recent studies have found that memory-based representations are not strictly co-localized with perceptual representations, but instead that information may transition from perceptual to memory-based representations moving anteriorly from areas of the scene-perception network[1,21–24]. Resolving this discrepancy is critical to understanding how contextual information from memory is brought to bear on visual representations in the brain. In short, do scene perception and place memory share common neural substrates?

Here, using fine-grained individual-subject fMRI, we reveal a network of brain areas that collectively bridge the scene perception and spatial memory systems of the human brain. In Experiment 1, we mapped the topology of scene-perception and place-memory related activity in 14 adult participants. We first independently localized the three regions of the scene-perception network[1] by comparing activation when participants viewed images of scenes, faces, and objects (Methods). Then, in the same participants, we localized areas that showed preferential BOLD-activation when participants recalled personally familiar places (e.g. their

house) versus faces (e.g. their mother)[22]. We subsequently compared activation between these two tasks.

This analysis revealed a striking topological pattern: in all participants, we found three clusters of place-memory activity in posterior cerebral cortex, each paired with one of the three scene-perception regions (Fig. 1). We henceforth refer to these previously undescribed regions as 'place-memory areas' for brevity. Across the lateral, ventral, and medial cortical surfaces, the pairs of place-memory and scene-perception areas exhibited a systematic topological relationship: the center-of-mass of each place-memory area was consistently anterior to the center-of-mass of its corresponding scene-perception area in every individual participant (Lateral pairs: $t(13)=16.41, p<0.0001, d=4.39$; Ventral pairs: $t(13)=12.115, p<0.0001, d=3.24$; Medial pairs: $t(13)=5.99, p<0.0001, d=1.6$; Extended data Fig. 1a; Supplementary File 1). Thus, adjacent, but dissociable brain areas support scene-perception and place-memory in posterior cerebral cortex.

In contrast to the striking distinction between scene perception and place memory, memory-related activation for faces was centered on the perceptually-driven FFA on the ventral surface ($t(9)=0.1211, p=0.906, d=0.17$), and we did not observe consistent memory-driven activation near the occipital face area on the lateral surface. The anterior shift for places was greater than that for faces on all surfaces (Main effect ROI: $F(3,85)=14.842, p<0.001$, t vs faces: all $ps<0.001$, all $ds > 2.26$). We reasoned that one potential explanation for the anterior distinction of memory and perception for scenes/places, but not faces might be the BOLD signal-dropout artifact affecting lateral ventral temporal cortex. However, we ruled out this explanation by replicating Experiment 1 using an advanced multi-echo fMRI sequence that improved signal from the lateral and anterior temporal lobe and obtaining similar results (Extended data Fig. 1b). Further, participants reported equal subjective vividness for place and face memory recall (Extended data Fig. 2). These findings show that place memory recall engages three distinct brain areas that are systematically adjacent and anterior to the scene-perception areas, and the consistent topological relationship between perception and memory was not true for faces.

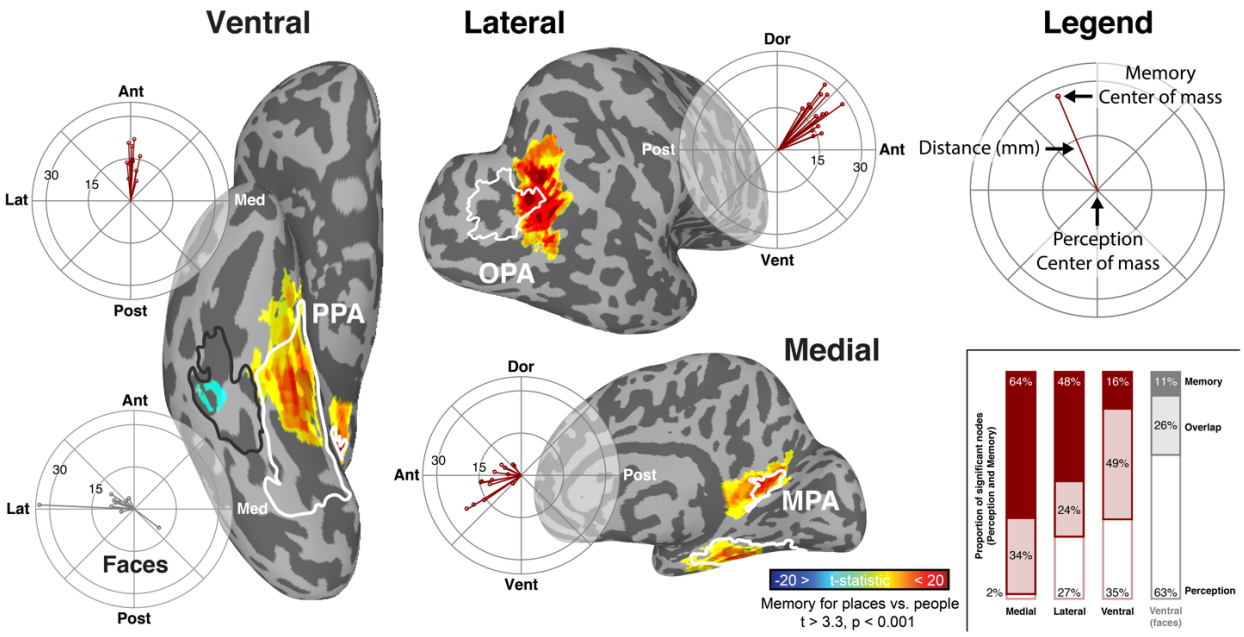

Fig. 1. Distinct topology of place-memory and scene-perception responses in posterior cerebral cortex. One example participant in Experiment 1 is shown (See Extended data Fig. 1 and Supplemental File 1 for thresholded and unthresholded activation maps for all participants (n=14)). The participant's scene perception ROIs are outlined in white, and place memory activity is shown in warm colors. The scene-perception network (parahippocampal place area [PPA], occipital place area [OPA], and medial place area [MPA) was localized by comparing the BOLD response when participants viewed images of scenes versus with faces (outlined in white, thresholded at vertex-wise $p < 0.001$). Place-memory areas on each surface were localized in separate fMRI runs by comparing the BOLD response when participants recalled personally familiar places versus people (warm colors, thresholded at vertex-wise $p < 0.001$). In all participants, three place-memory areas were observed, each located significantly anterior to one region of the scene-perception network. Polar plots: for each pair of regions, the center of mass of place-memory activation was significantly anterior to the center of mass of scene-perception activation in all participants (all ts > 5, $p < 0.001$). In contrast, face memory activation was spatially co-localized with the face-selective fusiform face area (FFA) on the ventral surface, and no anterior shift was observed (cool colors, $t_9 = 0.1211$, $p = 0.906$). Statistical analyses revealed no difference between the hemispheres, so, for clarity, only right hemisphere is shown. Inset: While the activation during place memory was systematically anterior to activation during scene perception, the spatial overlap between perception and memory activation varied across the cortical surfaces. Note that the axes (posterior-anterior) of each polar plot is aligned to its associated cortical surface.

We next asked whether this distinction between the place-memory and scene-perception areas is specific to top-down, constructive memory tasks like memory recall, or whether it extends to other classic memory paradigms that rely less on top-down signals (i.e. recognition memory). In Experiment 2, we compared responses of the place-memory areas with the scene-perception areas in a covert scene recognition task, wherein participants passively viewed panning movies of personally familiar and unfamiliar places (from Google StreetView; Supplemental Video 1-4; see Materials and Methods). Consistent with its role in recognition memory, the hippocampus

was driven by familiar vs. unfamiliar places ($F(1,39)=8.14$, $p=0.0069$, $t(13)=2.54$, $p=0.004$, $d=0.75$; Extended data Fig. 3a). Critically, the place-memory areas were also preferentially driven by familiar compared to unfamiliar places, significantly more so than the scene-perception areas (Region x Familiarity interaction – Lateral: $F(1,91)=20.98$, $p<0.001$, $t(13)=6.40$, $p<0.001$, $d=2.26$; Ventral: $F(1,91)=7.00$, $p=0.01$, $t(13)=4.443$, $p<0.001$, $d=1.55$; Medial: $F(1,91)=7.321$, $p=0.008$, $t(13)=7.19$, $d=1.05$; Fig. 2a,b). Importantly, the familiarity effect was not observed in the amygdala (Extended data Fig. 3b) or early visual cortex (Extended data Fig. 4), arguing against purely attention-related accounts of these effects. These data suggest that the place-memory areas are broadly driven by memory-related task demands, including both recall and recognition memory.

Real-world visual experience simultaneously taxes both perceptual analysis of scenes and memory of extended spatial environments. So, in Experiment 3 we examined the interaction of the place-memory and scene-perception areas under naturalistic conditions and characterized their network properties. Participants watched a movie designed to concurrently engage perceptual and mnemonic representations of complex real-world environments, and we analyzed the co-fluctuation of activity among the scene-perception and place-memory areas by calculating the correlation between the activity timeseries for each region pair, whilst accounting for the activation of all other regions (Fig. 2c). This analysis revealed that the place-memory areas constitute a distinct functional network, separate from the scene-perception network: the correlation among the scene-perception and place-memory areas (i.e., within network) was significantly greater than the correlation between these areas (i.e., between network) (Main effect Network: $F(60,2)=47.99$, $p<0.0001$; Perception:Perception v Perception:Memory, $t(12)=7.31$, $p<0.0001$, $d=4.63$; Memory:Memory v Perception:Memory $t(12)=5.31$, $p=0.0002$, $d=3.794$; Memory:Memory v Perception:Perception $t(12)=1.18$, $p=0.26$, $d=0.48$; Fig. 2d). Next, we assessed whether the scene-perception and place-memory areas respectively associate with the visual and spatio-mnemonic systems. Here, we observed a double dissociation (Main effect of Network: $F(3,84)=55.5$, $p<0.001$), whereby the scene-perception areas were more correlated to early visual cortex compared to the place-memory areas ($t(12)=6.05$, $p<0.001$, $d=4.26$), while the place-memory areas were more strongly correlated with the hippocampus ($t(12)=10.64$, $p<0.001$, $d=6.32$) (Fig. 2e). These data demonstrate that the place-memory areas constitute a distinct functional network, which closely associates with the hippocampus during naturalistic scene understanding.

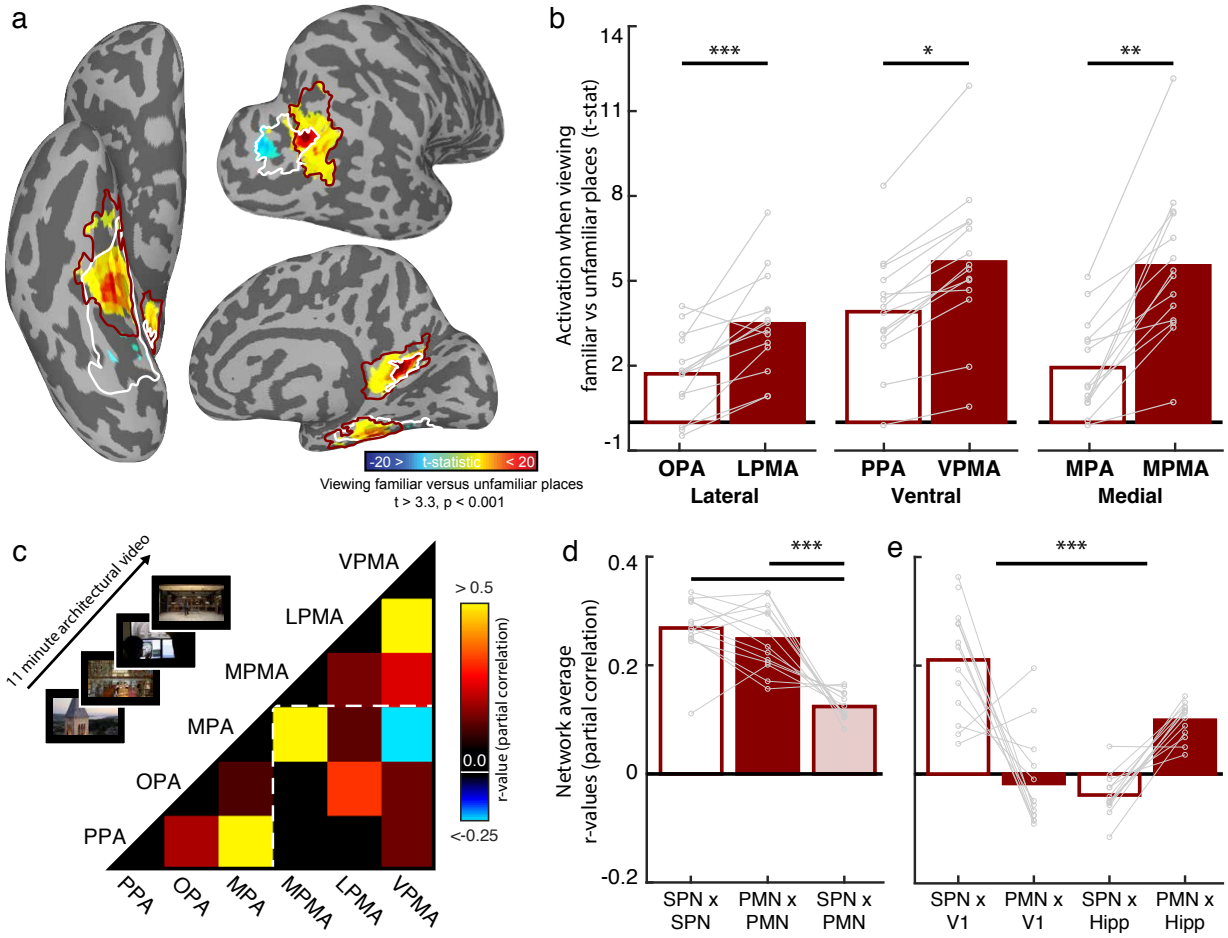

*Fig. 2. The place-memory areas respond preferentially to familiar stimuli and form a distinct functional network during scene-understanding***.** *a,b. The place-memory areas preferentially activate to familiar stimuli. a. Experiment 3. Participants viewed viewing panning movies of personally familiar places versus unfamiliar places, tailored to each participant using Google StreetView (see Supplemental Videos 1-4). The cortical surface depicts the contrast of BOLD activity for a single participant, thresholded at vertex-wise p < 0.001. Only significant vertices within the scene perception (white) and place memory (burgundy) areas are shown. b. Average t-statistic of vertices in the scene-perception (open bars) and place-memory areas (filled bars) when viewing videos of personally familiar places compared to unfamiliar places. On each cortical surface, the place-memory areas showed an enhanced response to familiar stimuli compared to the scene-perception areas (all ts > 2.6, ps < 0.01). Connected points depict individual participants. The hippocampus also showed a preferential response to familiar compared to unfamiliar place movies (Extended data Fig. 3a). The amygdala (Extended data Fig. 3b) and early visual cortex (Extended data Fig. 4) did not show a preferential response to familiar place movies, arguing against a purely attentional account of this effect. c-e. The place-memory areas constitute a distinct function network and associate closely with the hippocampus. c. Experiment 2. To assess whether the place-memory areas and scene-perception areas form distinct functional networks, participants watched an 11-minute video designed to elicit naturalistic scene understanding, comprised of several college admissions videos, real-estate listings, and architectural tours. For each participant (n=13), the average timeseries from the scene-perception areas (parahippocampal place area [PPA], occipital place area [OPA], and medial place area [MPA], the place-memory areas (medial, ventral, and lateral place memory areas [MPMA,*

*LPMA, VPMA]), and the pairwise partial correlation was calculated. The correlation matrix depicts the average partial correlation of each area from all participants (ordered by Ward similarity). d. The average pairwise partial correlation of within-network activity (Scene-perception network x Scene-perception network [SPN x SPN] and place-memory network x place memory network [PMN x PMN]) was significantly higher than the correlation of between network activity (SPN x PMN) ($F_{(2,60)}$=50.915, p<0.001). e. The scene-perception and place-memory areas differentially associate with the brain's visual and memory systems ($F_{(3,84)}$=55.5, p<0.001). The scene-perception areas were more correlated with early visual cortex (t_{12}=6.05, p<0.001), while the place-memory areas were more correlated with the hippocampus (t_{12}=10.64, p<0.001), which is further evidence for their roles in perception and memory, respectively. In all plots, n.s., p > 0.05; *p < 0.05; **p < 0.01; ***p < 0.001*

The discovery of a distinction between the functional networks supporting scene perception and place memory in posterior cerebral cortex is inconsistent with a classic theory in cognitive neuroscience: that perception and mental imagery of high-level visual stimuli engage the same neural circuitry[17–20,25,26]. In Experiment 4, we characterized the relative roles of the scene-perception and place-memory areas in mental imagery of visual scenes by directly comparing activity when participants performed mental imagery versus viewed panning movies of places (Fig. 3a). Consistent with our previous results, we found that mental imagery and perception differentially engage the place-memory and scene-perception areas (Network x Task interaction – Lateral: F(1,91)=237.37; p<0.001; Ventral: F(1,91)=78.19; p<0.001; Medial: F(1,91)=28.96; p<0.001). Specifically, we observed a double dissociation on all cortical surfaces. Compared to the place-memory areas, the scene-perception areas showed greater activation during perception than mental imagery (Lateral: t(13)=7.33; p<0.001, *d*=2.80; Ventral: t(13)=6.21, p<0.001, *d*=1.80; Medial: t(13)=4.15, p<0.001, d=0.97; Fig. 3b,c). In contrast, compared to the scene-perception areas, the place-memory areas were more active during mental imagery (Lateral: t(13)=8.35, p<0.001, *d*=3.33; Ventral: t(13)=6.63, p<0.001, *d*=2.44; Medial: t(13)=5.44, p<0.001, *d*=1.25; Fig. 3b, c). Remarkably, PPA, a region that prior studies found to be active during mental imagery[17], showed below-baseline activation during mental imagery (t(13)=-3.132, p=0.008), as did OPA (t(13)=-2.407, p=0.03). Within the scene-perception network, only MPA showed above-baseline activation during both mental imagery (t(13)=2.94, p=0.01) and perception (t(13)=4.89, p=0.003). Early visual cortex (Extended data Fig. 5), hippocampus (Extended data Fig. 6a), and amygdala (Extended data Fig. 6b) all showed greater activation during perception compared to imagery. These findings contradict the classic understanding that mental imagery recruits the same neural substrates as perception[17–20,25,26], and suggest that the place-memory network, not the scene-perception network, supports mental imagery of places.

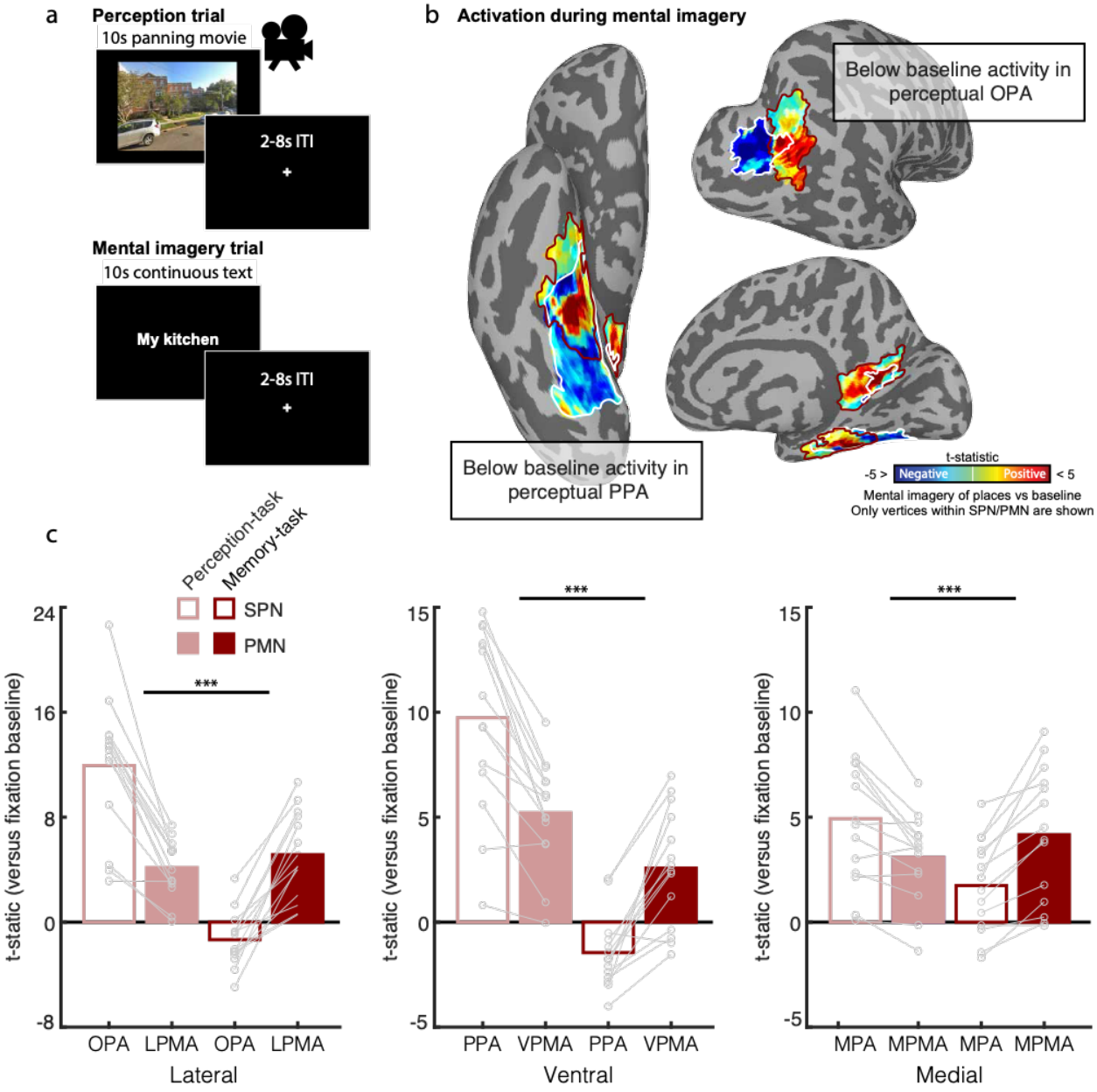

Figure 3. *Perception and mental imagery differentially engage the scene-perception and place-memory areas. a. In Experiment 4, participants (n = 14) saw panning movies of unfamiliar places (perception trials) or performed mental imagery of personally familiar places (mental imagery trials). b. BOLD activation during mental imagery of places compared to baseline for a representative subject. Below baseline activation within the perceptual areas PPA (ventral) and OPA (lateral) are highlighted. Only vertices within the scene-perception network (SPN; white) and place-memory network (PMN; burgundy) are shown. c. The scene-perception areas and place-memory areas are differentially engaged during scene perception and mental imagery. Activation versus baseline of the scene-perception (open bars) and place-memory areas (filled bars) during perception of places (pink) or mental imagery of places (red). A linear mixed effects model analysis revealed that on each cortical surface, there was a significant dissociation in activation during perception and mental imagery, where the scene perception areas were significantly*

*more active during perception, while the place memory areas were significantly more active during mental imagery of places (ROI x Task interaction – Lateral: $F_{(1,91)}$=237.37; p<0.001; Ventral: $F_{(1,91)}$=78.19; p<0.001; Medial: $F_{(1,91)}$=28.96; p<0.001). Early visual cortex (Extended data Fig. 5) and amygdala (Extended data Fig. 6) also showed below baseline responses during mental imagery; hippocampus responded more to perception compared to imagery, but positively in both conditions (Extended data Fig. 6). In all plots, n.s., p > 0.05; *p < 0.05; **p < 0.01; ***p < 0.001*

To summarize, our results show that scene perception and place memory are subserved by two distinct, but overlapping, functional networks in posterior cerebral cortex. The three regions of the place-memory network fall adjacent but anterior to regions of the scene-perception network on all three cortical surfaces – PPA (ventral), MPA (medial), and OPA (lateral) – and interface between scene perception and spatial memory systems in the human brain. Multiple recent studies have suggested that the anterior aspects of ventral temporal cortex, including PPA, harbor increasingly abstract[27] and context-related[24,28] information, consistent with their functional connectivity with memory structures[1,21–23,29] Our data situate these prior findings within a broader topographical organization of posterior cerebral cortex: place-selective memory areas lie immediately anterior to scene-selective visual areas on all three cortical surfaces. These findings reveal a new mechanistic step between the regions of the brain that support spatial memory and those that support visual scene analysis, closing a critical gap in our understanding of how contextual information from memory is brought to bear on visual representations in the brain.

The topological relationship between scene-perception and place-memory areas was strikingly consistent across individuals. All participants showed the characteristic posterior-anterior topographic relationship between scene-perception and place-memory selective activity. However, intriguingly, the degree of overlap varied systematically by cortical surface. Specifically, on the ventral surface, moving posteriorly to anteriorly there was a transition from an area activated during perception (PPA) to one activated by both perception and memory (ventral place memory area, VPMA). In contrast, on the medial surface, MPA was activated by both scene perception and place memory and was contained within a larger place-memory responsive area extending into medial parietal lobe (medial place memory area, MPMA). Only the lateral surface appeared to have a transition zone between an area only activated during perception (OPA), to one activated by both perception and memory, to one activated only during memory (lateral place memory area, LPMA). This systematic variation across the cortical surfaces was present in all participants (Supplemental File 1). Understanding this variable topology will likely be key to understanding these regions' differential contributions to memory-guided visual behavior.

Multiple aspects of our findings are surprising. First, based on previous fMRI studies, it has been widely assumed that perception and mental imagery of high-level stimuli (such as scenes) recruit the same neural substrates, including category-selective areas in ventral temporal cortex[17,25].

Interestingly, however, neuropsychological studies have suggested that mental imagery and visual recognition have dissociable neural substrates[30,31]. Our findings reconcile this discrepancy, by showing that distinct, but neighboring regions underlie perception and mental imagery of places. So, why might previous fMRI studies have reported that the substrates of perception and imagery in ventral temporal cortex are shared? First, the initial fMRI investigation into mental imagery and perception of high-level visual stimuli[17] used familiar exemplars for perception, which could recruit the VPMA (similar to Experiment 2 here). Second, this initial study, which used a combination of individual subject mapping and ROI analyses, reported that only a portion of PPA was active during imagery[17], but later studies did not investigate this distinction. So, the mental imagery-related activation and decoding observed in later studies (e.g. [19]) may also have arisen from nearby memory areas. Consistent with this hypothesis, we note that if we analyze PPA and VPMA combined as a single area, we find positive activation during mental imagery in the majority of our participants (Extended data Fig. 7). Third, typical whole-brain group-analyses could obscure the topological relationship between perception- and memory-related activity by averaging across individuals[18,20,26]. As such, our individualized analysis approach is uniquely suited to detect this fine-grained distinction.

A second notable finding is that the place memory network resides within the caudal inferior parietal lobule, medial temporal lobe, and posterior parietal cortex, which are hubs of the default mode network on the lateral, ventral, and medial surfaces, respectively[32]. Recent conceptualizations of human cortical organization consider these hubs as the apex of a macroscale gradient, spanning from unimodal (i.e. sensory or motor) areas to transmodal, high-level areas[33,34]. These transmodal areas are thought to facilitate cognitive processes, such as autobiographical memory, in a content-agnostic fashion[16,32,33,35–37]. Intriguingly, however, our data show that place-memory selective subregions exist within each of these default mode network hubs, broadly mirroring the category-selective subdivisions of the visual system[22,38,39]. Thus, we hypothesize that content-specificity may be a defining feature of cortical organization at each level of processing, even transmodal cortex. Neuropsychological patients support this assertion: damage to specific areas within the caudal inferior parietal lobule, posterior parietal cortex, or medial temporal lobe cause severe navigational impairments, while leaving other memory domains, such as face memory, intact[40,41]. This content-specific organization likely persists in prefrontal areas[42–44], although traditional functional imaging analysis approaches might fail to detect these tightly interdigitated features due to topographic heterogeneity across individuals[42–44]. Revealing these content-specific networks within individual participants will be paramount to understanding the neuroanatomical substrates underlying complex cognitive processes.

Finally, the distinct topology of perception and memory networks in posterior cerebral cortex was unique to the spatial domain – we found no separable networks for face-perception and memory. Why might a 'place-memory network', proximate to the scene-perception network,

exist, while an analogous 'face-memory network' does not? We hypothesize that the 'goal' of scene processing may be integrating the current field-of-view with the larger spatial context[24,45]. In contrast, the 'goal' of visual face processing is face recognition, which requires nuanced discrimination of a specific stimulus, but not broader context[6,46,47]. Consistent with this view, portions of the scene perception network can harbor representations of spatial context beyond the current field-of-view[24,45]. To conclude, we have described the place memory network: a set of brain areas in posterior cerebral cortex that support place memory recall. The discovery of these functionally distinct areas, residing between the brain's perception and memory systems, provides a new framework for considering the neural substrates of memory-guided visual behaviors.

Materials and Methods

Participants

Fourteen adults (9 females; age=25.7±3.6 STD years old) participated in the Experiments 1, 2, and 4. Of these, 13 participants took part in Experiment 3 (one participant requested to abort the scan; 8 females, age=25.9±3.6 STD years old). In addition, a subset of the original participants (N=6; 2 females, age=26.3±4.4 STD years old) completed the multi-echo replication of Experiment 1. Participants had normal or correct-to-normal vision, were not colorblind, and were free from neurological or psychiatric conditions. Written consent was obtained from all participants in accordance with the Declaration of Helsinki and with protocol approved by the Dartmouth College Institutional Review Board (Protocol #31288). We confirmed that participants were able to perform mental imagery by assessing performance Vividness of Visual Imagery Questionaire [48]. All participants score above 9 with eyes open, indicating satisfactory performance (mean=15.2, range=9.75-19.25).

Procedure

All participants took part in Experiments 1-4. In Experiment 1, we compared the topology of activation i) during a scene/face perceptual localizers with ii) the topology of place/people memory-recall related activation collected in separate fMRI runs. In Experiment 2, we investigated the involvement of the place-memory areas to recognition memory by comparing activation when participants viewed panning movies of personally familiar and unfamiliar places. In Experiment 3, we investigated the relationship between the scene-perception and place-memory areas under naturalistic conditions by evaluating the correlated activity of these areas during a movie watching task. Finally, in Experiment 4, we evaluated the relative involvement of the scene-perception and place-memory areas to perception and mental imagery by evaluating

their activation when participants performed mental imagery of personally familiar places and viewed panning videos of unfamiliar places.

Personally familiar stimulus generation

Mental imagery stimuli

In order to localize memory responsive areas (Experiment 1) and the mental imagery versus perception experiment (Experiment 4), we asked participants to generate a list of 36 familiar people and places (72 stimuli total). These stimuli were generated prior to scanning based on the following instructions:

For your scan, you will be asked to visualize people and places that are personally familiar to you. So, we need you to provide these lists for us. For personally familiar people, please choose people that you know personally (no celebrities) that you can visualize in great detail. You do not need to be in contact with these people now – just as long as you knew them personally and remember what they look like. So, you could choose your childhood friend even if you are no longer in touch with this person. Likewise, for personally familiar places, please list places that you have been to and can imagine in great detail. You should choose places that are personally relevant to you, so you should avoid choosing places that you have only been one time, and you should not choose famous places where you have never been. You can choose places that span your whole life, so you could do your current kitchen as well as the kitchen from your childhood home.

Familiar panning movie stimuli

To generate panning movies of personally familiar places for Experiment 2, participants used the GoogleMaps plug-in iStreetView (istreetview.com) to locate and download 24 photospheres of personally familiar places based on the following instructions:

In another part of your scan, you will see videos of places that will be familiar or unfamiliar to you. You will use iStreetView to locate places with which you are familiar. iStreetView has access to all photospheres that Google has access to, as well as all of the photospheres from Google Street View. So, you should do your best to find photospheres taken from perspectives where you have actually stood in your life. Like before, please find places that are personally familiar to you (such as in front of your childhood school), rather than famous places (like the Eiffel tower), even if you have been to that famous place in your life.

Participants were also asked to specify whether a particular viewpoint would be most recognizable to them so that this field-of-view could be included in the panning movie. Once the photospheres were chosen, panning movies were generated by concatenating a series of 90° fields-of-view images taken from the photospheres that panning 120° to the right (in steps of 0.4°), then back to the left. The videos always began and ended at the same point of view, and

the duration of the video was 10 seconds. Supplemental Videos 1-4 show examples of these videos.

Perceptual category localizer

Face- and scene-selective perceptual areas were localized using a block-design functional localizer. Participants were shown images of faces, scenes, and objects (image presentation duration: 500 ms; ISI: 500 ms; block duration: 24 s; number of blocks per condition: 6). Blocks were presented continuously with no baseline periods between blocks. Participants were instructed to passively view the images and performed no task during the perceptual localizer experiment. Two runs of the localizer were performed.

Memory activation localizer

People and place selective memory activation was localized using a procedure adapted from [22]. Participants were shown written names of 36 personally familiar people and 36 places that they provided to us prior to the MRI scan. The task was performed over 4 runs, with 9 people and place stimuli presented during each run in a pseudo-randomized order. No more than 3 instances of a stimulus category (i.e. person or place) could appear consecutively.

During the task, participants were instructed to visualize the stimulus from memory as vividly as possible for the duration of the trial (10 s) following the instructions detailed below. Trials were separated by a variable inter-trial interval (4-8 s).

The instructions were as follows:

In this task, you will see the name of a person or place from the list you provided us. When the name appears, I want you to perform memory recall of that stimulus. The recall should be as vivid as possible, and you should try to do this the whole time that the name is on the screen.

If the name you see is a person, I want you to imagine that person's face in as much detail as possible. You should picture their head in front of you as the person turns their head from left to right and up and down, so that you can see all of the sides of their face. They can make different expressions, as well.

The most important thing is that you are picturing their face; when some people perform memory recall, they will imagine interacting with that person or touching and hugging them. We do not want you to do this, just imagine the face. Also, do not picture their bodies, arms, or legs. Try to focus just on their face as it moves in your mind's eye.

If the name you see is a place, I want you to imagine that you are in the place. You should direct your attention around the place, looking to the left and right of you, and looking up and down, and behind you. We want you to have the experience of being in this place as much as possible.

When you are imagining places, you should imagine yourself standing in one single spot. Don't walk around the place or imagine yourself from above. Also, we want it to be as though you are in the place, rather than thinking about the objects in the place. So, as you "look" around, don't think about the individual objects or list them in your mind. Instead, we want you to image that the place has materialized all around you, and all of the things that would be within your field of view are "visible" at the same time. For example, if you are imagining your kitchen, do not imagine the chairs, table, and windows sequentially. Instead, try to imagine all of these features at once, and that you're looking around and experiencing them as you would if you were in the room.

Between each trial, participants were instructed to clear their mind, relax, and wait for the next trial to begin.

Familiar/unfamiliar places experiment

The goal of Experiment 2 was to determine whether the place memory areas respond preferentially to familiar stimuli (i.e. stimuli that could be recognized) presented visually. To this end, we compared brain activation when participants saw panning videos of personally familiar places with activation when viewing videos of unfamiliar places. Familiar videos were taken from photospheres as described above. Unfamiliar videos were randomly sampled from other participants. Videos of Dartmouth College and Hanover, NH were excluded from the possible unfamiliar places.

The experiment was performed across 6 runs, with each run featuring 8 familiar and 8 unfamiliar place videos. There were 24 videos in each condition, and each video was seen twice. Before the experiment, participants were told that they would be seeing videos of familiar and unfamiliar places panning from left to right, then back again and that they should imagine that they were standing in that place, turning their head like the video. The instructions provided to the participants are reproduced below.

You will see panning movies of places that you are familiar with, as well as places that will not be familiar to you. Regardless of which you see, we want you to imagine that you are in that location and the video is your perspective as you turn your head from left to right, and back again. You should not actually turn your head.

Be sure that for all scenes you are pretending you are in that location, whether or not they are familiar to you. Of course, if it is a familiar location, you might be able to predict what is coming into view. That is fine, just do your best to imagine you're in that place for both conditions.

Each trial lasted 10 seconds. Trials were separated by a variable inter-trial interval (4-8 s). All videos were repeated two times in the experiment: once in the first three runs, and once in the last three runs.

Naturalistic movie watching experiment

To determine how the scene-perception and place-memory areas respond during naturalistic conditions, 13 participants took part in a movie watching experiment. No audio was included in the video. We chose a natural movie watching task, rather than a simple resting-state scan, to avoid the possibility that mind-wandering or mental imagery might cause a decoupling of the perception and memory networks artificially[35,49].

The movie consisted of an architectural tour, three college admissions videos, one tourism informational video, and one real-estate listing downloaded from YouTube. Specifically, the segments were: 1) an architectural tour of Moosilauke Ravine Lodge in Warren, NH (0:00-2:00), 2) an admission video of Princeton University in Princeton, NJ (2:00-3:00), 3) an admission video of Dartmouth College in Hanover, NH (3:00-3:51), 4) an admission video of Cornell University in Ithaca, NY (3:52-6:40), 5) a tourism informational video of the University of Oxford in Oxford, United Kingdom (6:40-8:53), 6) and a real-estate listing of a lake front property in Enfield, NH (8:53-11:00). Each segment included footage of people and places, ground-level and aerial footage, and indoor and outdoor footage. Videos were chosen to match closely for content, footage type, and video quality, while varying in the degree to which participants would be familiar with the places. Participants were not asked whether places were familiar to them. The full video can be found here: https://bit.ly/2Arl3I0.

Mental imagery versus perception experiment

Experiment 4 explicitly tested whether the place memory network was activated to a greater extent than the scene perception network during mental imagery. Each imaging run featured two types of trials, perception and mental imagery trials. On perception trials, participants saw a panning movie of an unfamiliar place, and were instructed to imagine that they were in that place turning their head (as in Experiment 3). On mental imagery trials, participants saw the name of a personally familiar place, and performed mental imagery of that place following the instructions given in Experiment 1. This task was presented over 6 runs. Each run featured 8 familiar place word stimuli for mental imagery and 8 unfamiliar place videos. As in Experiment 3, 24 unique stimuli were used in each condition (24 place word stimuli taken from the list generated in Experiment 1, and 24 panning videos of unfamiliar places). Trials lasted 10 s and were separated by a variable inter-trial interval (4-8 s). All stimuli were repeated two times in the experiment, once in the first three runs, and once in the last three runs.

MRI acquisition and preprocessing

All data was collected on a Siemens Prisma 3T MRI scanner equipped with a 32-channel head coil at Dartmouth College. Images were transformed from dicom to nifti files using dcm2niix [50], which applies slice time correction by default.

T1 image

For registration purposes, a high-resolution T1-weighted magnetization-prepared rapid acquisition gradient echo (MPRAGE) imaging sequence was acquired (TR=2300 ms, TE=2.32 ms, inversion time=933 ms, Flip angle=8°, FOV=256 x 256 mm, slices=255, voxel size=1 x 1 x 1 mm). T1 images segmented and surfaces were generated using Freesurfer[51–53].

Single-echo fMRI

Acquisition

In Experiments 1-4, single-echo T2*-weighted echo-planar images covering the temporal, parietal, and frontal cortices were acquired the following parameters: TR=2000 ms, TE=32 ms, GRAPPA=2, Flip angle=75°, FOV=240 x 240 mm, Matrix size=80 x 80, slices=34, voxel size=3 x 3 x 3 mm. To minimize dropout caused by the ear canals, slices were oriented parallel to temporal lobe[54]. The initial two frames were discarded by the scanner to achieve steady state.

Preprocessing

Task fMRI (Experiments 1, 3, and 4)

Task fMRI data was preprocessed using AFNI[55]. In addition to the frames discarded by the fMRI scanner during acquisition, the initial two frames were discarded to allow T1 signal to achieve steady state. Signal outliers were attenuated (3dDespike). Motion correction was applied, and parameters were stored for use as nuisance regressors (3dVolreg). Data were then iteratively smoothed to achieve a uniform smoothness of 5mm FWHM (3dBlurToFWHM).

Naturalistic movie watching (Experiment 2)

Naturalistic movie watching data were preprocessed using a combination of AFNI and FSL tools. Signal outliers were attenuated (3dDespike). Motion correction was applied. Data were then iteratively smoothed to achieve a uniform smoothness of 5mm FWHM (3dBlurToFWHM).

For denoising, independent component analysis (ICA) was applied to decompose the data into signals and sources using FSL's melodic[56–58]. These were classified as signal or noise by one investigator (AS) using the approach described in Griffanti et al. (2014)[59]. Components classified as noise were then regressed out of the data (fsl_regfilt). Motion from volume registration was not included in the regression, as motion is generally well captured by the ICA decomposition[59].

Time series were then transferred to the high-density suma standard mesh (std.141) using @SUMA_Make_Spec_FS and @Suma_AlignToExperiment.

Multi-echo fMRI

Acquisition

To better characterize activation during mental imagery of personally familiar people, we acquired a replication dataset of Experiment 1 using a multi-echo T2*-weighted sequence. Multi-echo imaging afforded the benefit of mitigating dropout with short echo times, while maintaining a high level of BOLD contrast with long echo times[60–62]. The sequence parameters were: TR=2000 ms, TEs=[11.00, 25.33, 39.66, 53.99 ms], GRAPPA=3, Flip angle=75, FOV=240 x 240 mm, Matrix size=80 x 80, slices=40, Multi-band factor=2, voxel size=3 x 3 x 3 mm. As with single-echo acquisition, the slices were oriented parallel to the temporal lobe. The initial two frames were discarded by the scanner.

Preprocessing

Multi-echo data preprocessing was implemented based on the multi-echo preprocessing pipeline from afni_proc.py. Initial preprocessing steps were carried out on each echo separately. Signal outliers were attenuated (3dDespike). Motion correction parameters were estimated from the second echo (3dVolreg); these alignment parameters were then applied to all echoes.

Data were then denoised using multi-echo ICA (tedana.py[61–63]). The optimal combination of the four echoes was calculated, and the echoes were combined to form a single, optimally weighted time series (T2smap.py). Data were then subjected to PCA, and thermal noise was removed using the Kundu decision tree, which selectively eliminates components that explain a small amount of variance and do not have a TE-dependent signal decay across echoes. Subsequently, ICA was performed to separate the time series into independent spatial components and their associated signals. These components were classified as signal and noise based on known properties of the T2* signal decay of BOLD versus noise. The retained components were then recombined to construct the optimally combined, denoised time series. Following denoising, images were blurred with a 5mm gaussian kernel (3dBlurInMask) and normalized to percent signal change.

fMRI analysis

Region of interest definitions

To define category selective perceptual areas, the scene perception localizer was modeled by fitting gamma function of the trial duration with a square wave for each condition (Scenes, Faces, and Objects) using 3dDeconvolve. Estimated motion parameters were included as additional regressors of no-interest. To compensate for slow signal drift, 4th order polynomials were

included for single-echo data. Polynomial regressors were not included multiecho data analysis. Scene and face areas were drawn based on a general linear test comparing the coefficients of the GLM during scene and face trials. These contrast maps were then transferred to the suma standard mesh (std.141) using @SUMA_Make_Spec_FS and @Suma_AlignToExperiment. A vertex-wise significance of $p<0.001$ along with expected anatomical locations was used to define the regions of interest – in particular, visually responsive PPA was not permitted to extend posteriorly beyond the fusiform gyrus.

To define category-selective memory areas, the familiar people/places memory data was modeled by fitting a gamma function of the trial duration for trials of each condition (people and places) using 3dDeconvolve. Estimated motion parameters were included as additional regressors of no-interest. To compensate for slow signal drift, 4th order polynomials were included for single-echo data. Polynomial regressors were not included multiecho data analysis. Activation maps were then transferred to the suma standard mesh (std.141) using @SUMA_Make_Spec_FS and @Suma_AlignToExperiment. People and place memory areas were drawn based on a general linear test comparing coefficients of the GLM for people and place memory. A vertex-wise significance threshold of $p<0.001$ was used to draw ROIs.

To control for possible signal-to-noise differences introduced by variably sized ROIs, for analysis of correlated activity during movie watching (Experiment 3) and activation in Experiments 2 and 4, scene-perception and place-memory ROIs were constrained to unique members of the top 300 vertices from the perception and memory areas. These ROIs are referred to as "constrained ROIs" in subsequent sections.

Analysis of topology of perception and memory areas

The topology of the perception and memory areas was compared in two ways: by identifying whether there was a significant anterior shift from perception to memory and quantifying the overlap between category selective perception and memory vertices at the significant threshold $p<0.001$.

To quantify the anterior displacement of perception and memory areas, we calculated the weighted center of mass for the scene-perception/place-memory selective area on each surface, where the contribution of each vertex to the center of mass was weighted by its selectivity (t-statistic). The distance between the center of mass for perception and memory in the y-dimension (posterior-anterior) was then compared using a linear mixed effects model with ROI (perception/memory) and Hemisphere (lh/rh) as factors separately for each surface. Because there was no significant effect of hemisphere, the data are presented collapsed across hemisphere (all $ps>0.10$). In addition, to determine whether the anterior displacement of memory compared to perception was specific to scenes, we compared the distance in the y direction between the PPA and ventral place memory area (VPMA) with the FFA and the face-

memory selectivity are on the ventral surface using a linear mixed effects model with Category (scene/face), ROI (perception/memory) and Hemisphere (lh/rh) as factors.

To further examine the relationship between perception and memory on each surface, we then qualitatively compared the overlap between the category-selective perception and memory areas on each surface.

Activation analyses (Experiments 2 & 4)

For Experiments 2 and 4, a gamma function of duration 10s was used to model responses for trials in each condition (Experiment 2: familiar/unfamiliar places videos; Experiment 4: mental imagery/perception). These regressors, along with motion parameters and 4th order polynomials were fit using 3dDeconvolve. Activation maps were then transferred to the SUMA standard mesh (std.141) using @SUMA_Make_Spec_FS and @SUMA_AlignToExperiment.

For analysis, the average t-statistic (compared to baseline) for each condition (Experiment 3: familiar versus unfamiliar videos; Experiment 4: mental imagery versus perception tasks) from the constrained ROIs was calculated. The average t-statistics were compared using a linear mixed effects model [64] in R [65] for each surface separately (i.e. PPA v VPMA, MPA v MPMA, OPA v LPMA were separately compared). Trial condition (Experiment 3 – Familiarity: familiar/unfamiliar; Experiment 4 – Task: perception/imagery) and Hemisphere (lh/rh) were included as factors. There was no significant effect of hemisphere in any test, and thus data are presented collapsed across hemisphere (all ps>0.10). Post-hoc tests were implemented using the emmeans package [66]. In addition, to determine whether a region was significantly active above or below baseline, the t-static from each ROI was compared versus zero. T-statistics were chosen to aid comparison across areas, which is typical in these studies[6].

Analysis of correlated activity timeseries during movie watching

For analysis of the co-fluctuation of activity patterns during movie watching, for each participant, we first extracted the average time course of each constrained ROI, as well as the hippocampus and early visual cortex, which were anatomically defined based on each participant's FreeSurfer segmentation/parcellation. We then calculated the correlation of the time series from each region pair while partialing out the time series from all other region pairs. The correlation matrices were calculated for each hemisphere separately. The average pairwise correlation within- and between- networks (perception: PPA, MPA, OPA; memory: VPMA, medial place memory area (MPMA), and lateral place memory area (LPMA)) were then compared using a linear mixed effects model with Connection (PxP, MxM, and PxM) and Hemisphere (lh/rh) as factors. The average correlation of each network with hippocampus and early visual cortex was compared using a linear mixed effects model [64] with Network (Perception/Memory) and Hemisphere (lh/rh) as factors. Significant model terms were determined using an analysis of

variance implemented in R[65]. There was no significant effect of hemisphere in any test, and thus data are presented collapsed across hemisphere (all ps>0.10).

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A network linking perception and memory systems in posterior cerebral cortex.

Supplemental material

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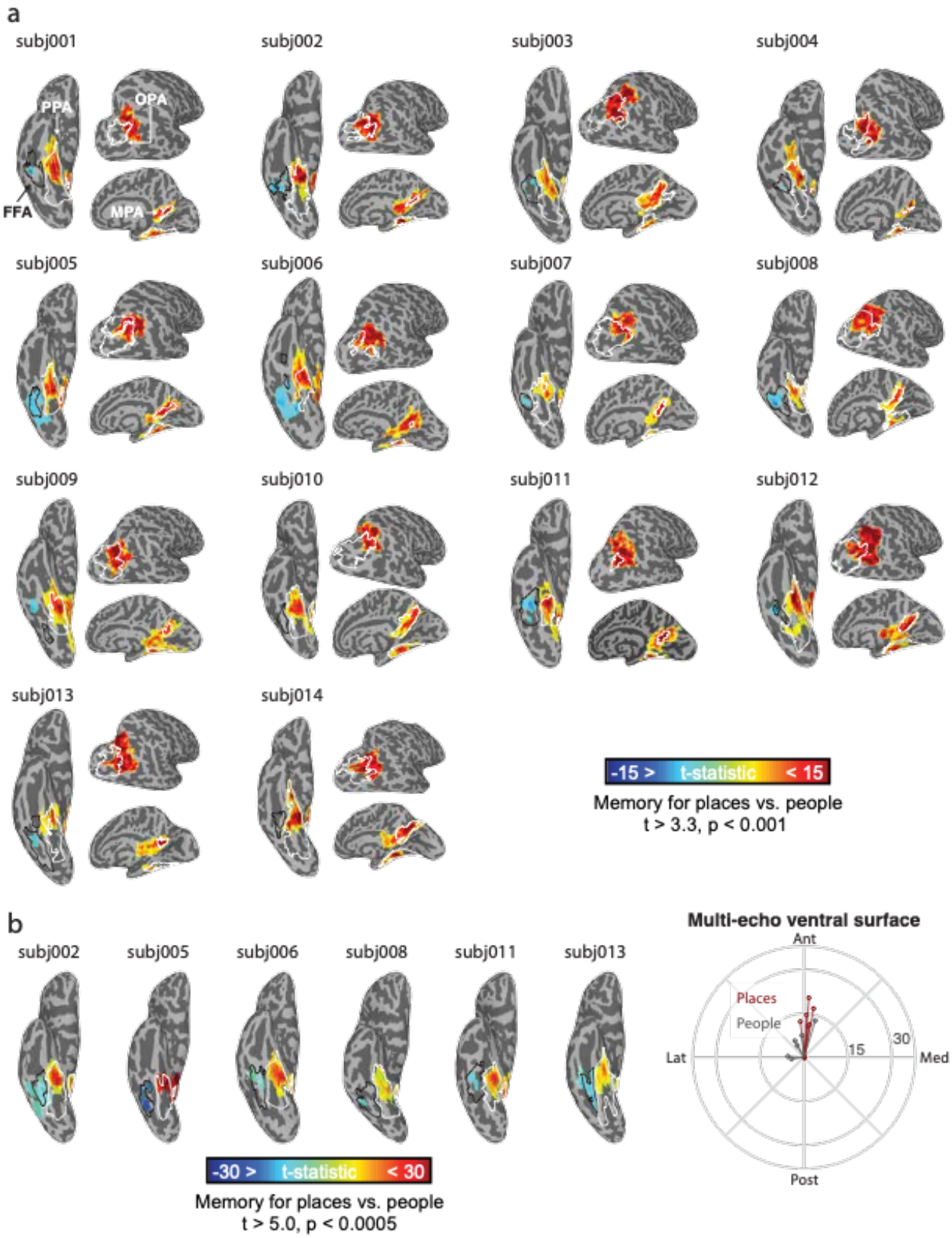
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-15 > t-statistic < 15
Memory for places vs. people
t > 3.3, p < 0.001
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-30 > t-statistic < 30
Memory for places vs. people
t > 5.0, p < 0.0005
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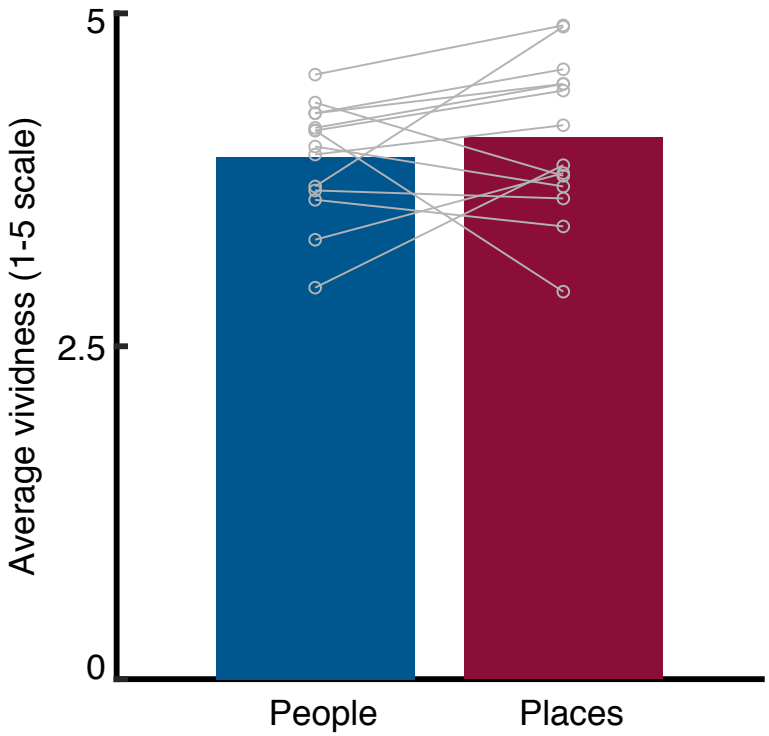
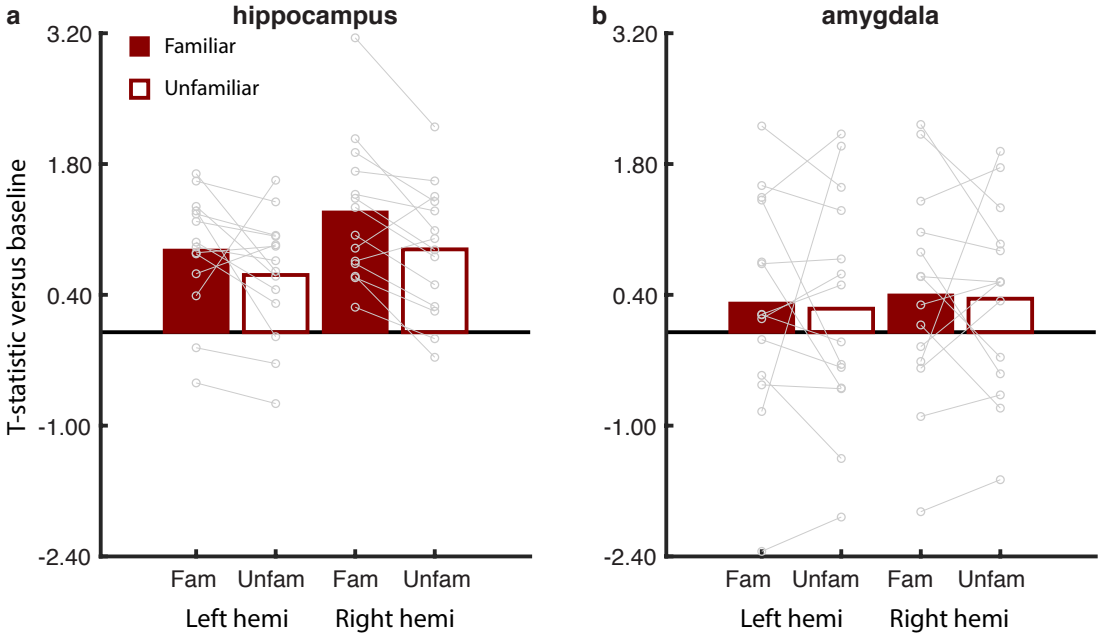
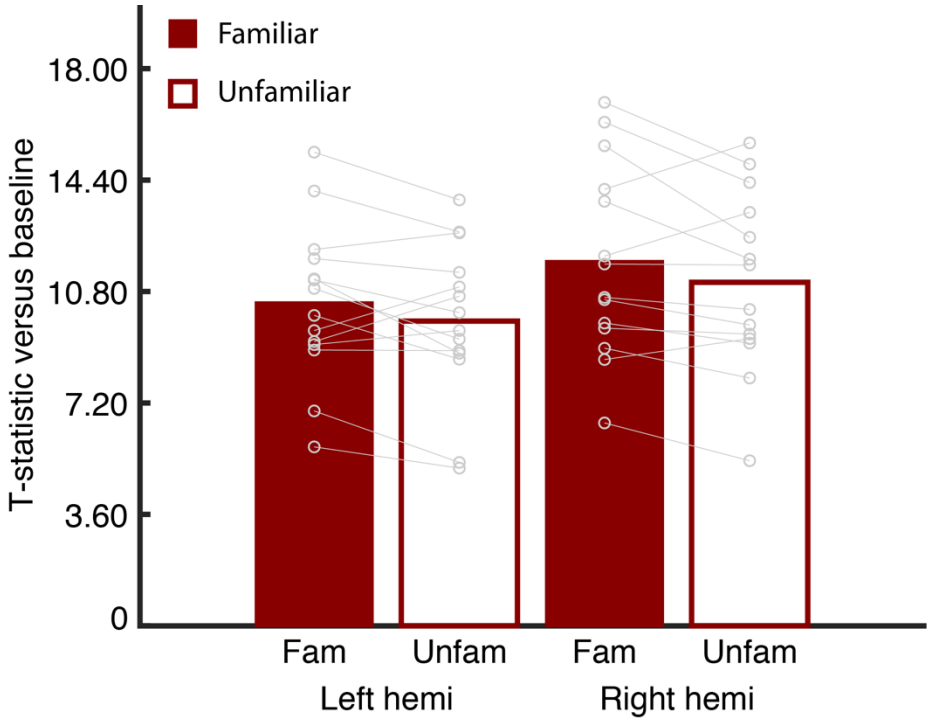
Extended data Fig. 1. Place-memory selective activation is anterior to scene-selective perceptual activation in all participants. *a. In each participant, scene-selective perceptual areas (parahippocampal place area [PPA], occipital place area [OPA], and medial place area [MPA]) were localized by comparing BOLD activation when viewing images of places compared to people); the white outlined region shows each scene-selective area (PPA, OPA, MPA) thresholded at vertex-wise $p < 0.001$. Place-memory selective areas were localized by comparing BOLD activation when participants recalled personally familiar places versus personally familiar faces. These maps were thresholded at vertex-wise $p < 0.001$. In all participants, on cortical surface the memory activation falls significantly anterior to scene perception activation. Face-selective perception (grey outline) and face-selective memory (cool colors) areas on the ventral surface are shown for comparison thresholded at (vertex-wise $p < 0.001$). At this threshold, people-memory activation on the ventral surface was only visible in 12/14 participants on the right hemisphere and 13/14 participants in the left hemisphere (not shown). In contrast to scene areas, the center of mass of people-memory was not anterior to face-perception. b. Signal dropout from the air-tissue interface of the ear canal is known to obscure activity in the lateral and anterior temporal lobe, and therefore could prevent us from observing an anterior bias during face memory recall activity relative to perception of faces. To ensure this was not the case, we replicated the comparison of perception and memory localizers using multi-echo fMRI in a subset of participants, with a short-TE (11 ms) to mitigate the dropout artifact [1–3]. We were able to replicate the anterior bias in place-memory selective activation (relative to activation during scene-perception) in the replication cohort. In addition, we did not observe any consistent anterior bias for people memory activation relative to activation during face perception. All participants unthresholded activation maps for both perception and memory localizers can be found in Supplemental File 1.*



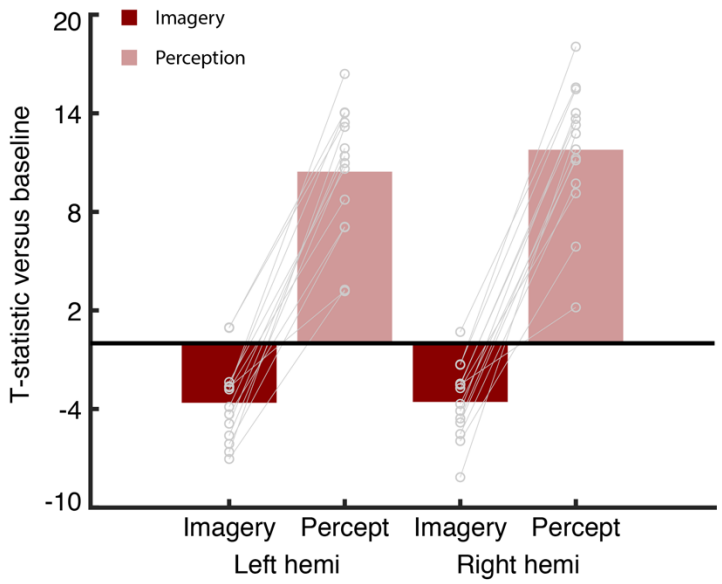
Extended data Fig. 2. Participants reported no difference in vividness between imagery for people and places. *Outside of the scanner, participants rated each personally familiar stimulus for vividness of visual imagery on a scale of 1-5, where 1 indicates no imagery possible and 5 indicates "as if you were seeing the <stimulus>." There was no significant difference in vividness between people and place stimuli (t(13) = 0.92, p = 0.373), suggesting that the topological difference between place and people imagery activation was not due to differences of vividness between the stimulus categories.*



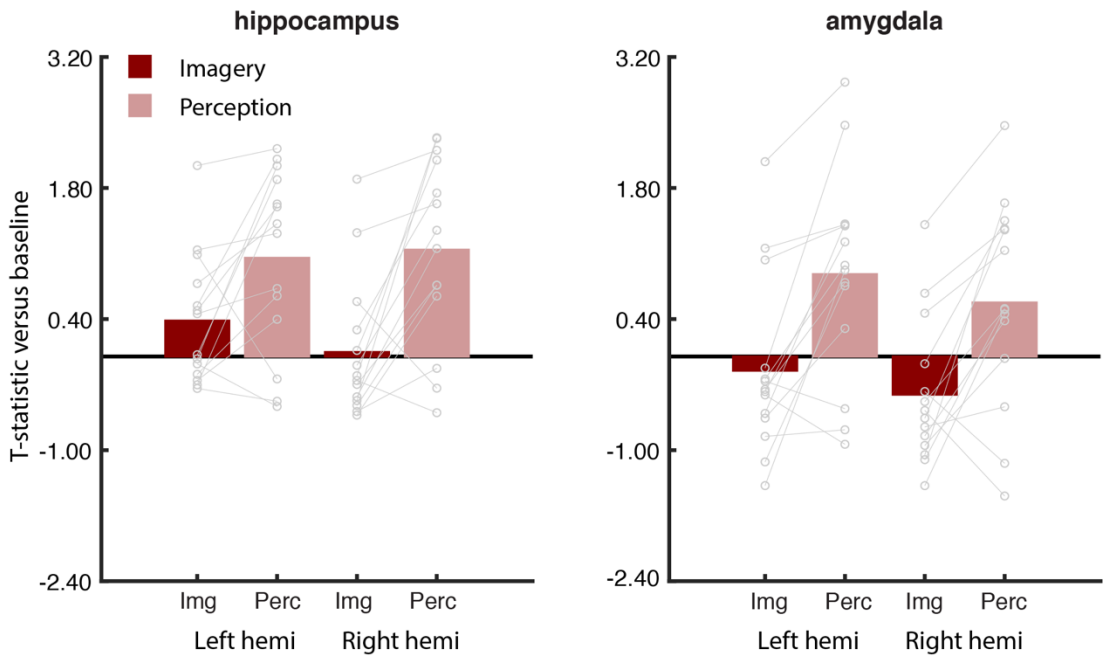
Extended data Fig. 3. Hippocampus responds preferentially to familiar place movies, while amygdala does not. *As an exploratory analysis, we tested how the hippocampus, which we expected would preferentially respond to familiar images, responded in Experiment 2, where participants viewed familiar and unfamiliar panning movies. The average T-statistic from all voxels within the hippocampus and amygdala (defined by Freesurfer segmentation) was extracted for each participant. We then compared the activation for each region separately using a linear mixed effects model with Hemisphere (left/right) and Familiarity (familiar/unfamiliar) as factors. a. As predicted, the hippocampus preferentially activated to familiar compared to unfamiliar stimuli (Main effect of Familiarity: $F(1,39)=8.14$, $p = 0.0069$; $t(13)=2.54$, $p = 0.004$). Activation was stronger in the right hemisphere compared to the left hemisphere (Main effect of Hemisphere: $F(1,39)=8.61$, $p = 0.0056$; $t(13)=2.38$, $p=0.0055$); however, there was no interaction between Hemisphere and Familiarity (Hemisphere x Familiarity interaction: $F(1,39)=0.33$, $p = 0.56$). b. In contrast, in the amygdala, there was no effect of Familiarity ($F(1,39)=0.29$, $p = 0.59$), Hemisphere ($F(1,39)=0.07$, $p = 0.78$), or interaction between Hemisphere and Familiarity ($F(1,39)=0.003$, $p = 0.95$), arguing against a simple account of attention modulating the response to familiar compared to unfamiliar stimuli.*



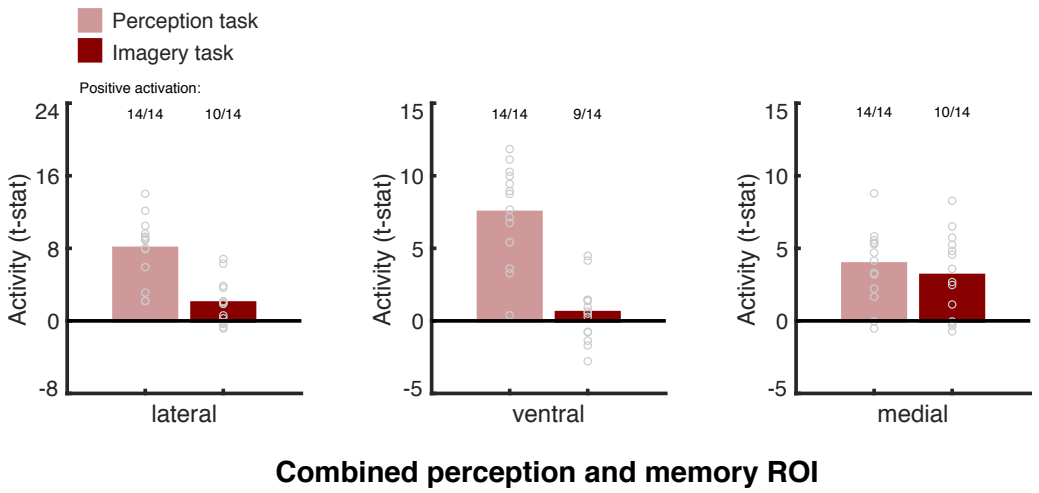
Extended data Fig. 4. Early visual cortex responses to familiar and unfamiliar place movies do not differ. *One explanation for the increased activation to familiar compared to unfamiliar stimuli is that greater attention is being paid to familiar stimuli, causing a global increase in activation of visually-responsive areas. To confirm that this was not the case, we compared activation of the occipital pole (defined in each participant from their Freesurfer parcellation) when participants viewed familiar versus unfamiliar panning movies. We compared the responses using a mixed effects model with Hemisphere (lh/rh) and Familiarity (familiar/unfamiliar) as factors. We found that responses in the right hemisphere were stronger than the left hemisphere (Main effect of Hemisphere: $F(1,39) = 13.29$, $p = 0.0008$; $t39=3.65$, $p = 0.0008$). However, we found no effect of Familiarity ($F(1,39)=3.19$, $p = 0.08$) or interaction between Hemisphere and Familiarity ($F(1,39)=0.01$, $p = 0.91$), confirming that a simple attentional account cannot explain the familiarity effect observed in the place-memory areas.*



Extended data Fig. 5. Early visual cortex responds more strongly to perception than mental imagery*. As an exploratory analysis, we investigated the response in early visual cortex (occipital pole defined in individual participants from their Freesurfer segmentation) during perception of unfamiliar places and mental imagery of familiar places. We compared the responses using a mixed effects model with Hemisphere (lh/rh) and Task (imagery/perception) as factors. As expected, we found that early visual cortex responded significantly more to perception compared to mental imagery (Main effect of Task: $F(1,39) = 541.38$, $p < 0.0001$; $t(13) = 16.83$, $p < 0.0001$). There was no effect of Hemisphere ($F(1,39) = 1.22$, $p = 0.22$) or interaction between Hemisphere and Task ($F(1,39) = 1.05$, $p = 0.31$).*



Extended data Fig. 6. Both hippocampus and amygdala respond more strongly during perception compared to mental imagery. *As an exploratory analysis, we investigated whether the hippocampus and amygdala — subcortical areas implicated in memory processes — responded differently when viewing panning movies of unfamiliar places and mental imagery of familiar places. The average T-statistic from all voxels within the hippocampus and amygdala (defined by Freesurfer segmentation) was extracted for each participant. We then separately compared the activation of each region using a linear mixed effects model with Hemisphere (left/right) and Task (Imagery/Perception) as factors. Both the hippocampus and amygdala responded more strongly during perception compared to mental imagery (Hippocampus: $F(1,39)=28.67$, $p < 0.0001$ $t(13)=3.31$, $p < 0.0001$; Amygdala: $F(1,39)=37.22$, $p < 0.0001$; $t(13)=4.01$, $p < 0.0001$). Responses did not differ by hemisphere in either region (Hippocampus: $F(1,39)=0.57$, $p = 0.45$; Amygdala: $F(1,39)=2.86$, $p = 0.09$), and there was no interaction between Hemisphere and Task in either region (Hippocampus: $F(1,39)=1.65$, $p = 0.20$; Amygdala: $F(1,39)=0.02$, $p = 0.89$).*



Extended data Fig. 7. All cortical surfaces (lateral, ventral, medial) show positive activation during perception and imagery when scene-perception and place-memory areas are considered together. *Previous studies of mental imagery (e.g. [4]), have found that mental imagery and perception activate shared neural substrates. However, these studies have not considered the scene-perception and place-memory areas separately. Therefore, in order to relate our results to previous studies of mental imagery, the average t-statistic of the scene-perception and place-memory areas from each cortical surface were extracted and combined into a single "combined ROI". Consistent with prior work, we found that mental imagery positively activated the combined ROI in the majority of participants (lateral: 10/14, mean t-stat = 1.96; ventral: 9/14, mean t-stat = 0.56; medial: 10/14, mean t-stat = 3.12). Group activation of the lateral (t(13) = 2.99, p = 0.011) and medial (t(13) = 4.08, p = 0.0013) surfaces were significantly above zero during mental imagery. Despite the majority of participants showing positive activation, the ventral surface was not significantly above zero at the group level (t(13) = 1.03, p = 0.32).*

Supplemental File 1. All participants unthresholded activation maps. This file is a gif image displaying, alternatingly, the unthresholded activation maps for the scene perception (perception of scene versus faces) and place memory (memory recall of places versus people) localizer tasks. The anterior shift of memory relative to perception can be seen in all participants. Note that, for clarity, only the right hemisphere is shown because no significant interaction with hemisphere was found.

Supplemental Video 1. Example panning video of a familiar outdoor place used in Experiments 2 and 4 (Oxford, United Kingdom).

Supplemental Video 2. Example panning video of a familiar indoor place used in Experiments 2 and 4 (Hanover, NH, United States).

Supplemental Video 3. Example panning video of a familiar city street used in Experiments 2 and 4 (Yongkang, Zhejiang, China).

Supplemental Video 4. Example panning video of a familiar place used in Experiments 2 and 4 (Zandvoort, Netherlands).

References

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2. Kundu, P., Inati, S. J., Evans, J. W., Luh, W. M. & Bandettini, P. A. Differentiating BOLD and non-BOLD signals in fMRI time series using multi-echo EPI. *Neuroimage* **60**, 1759–1770 (2012).

3. Evans, J. W., Kundu, P., Horovitz, S. G. & Bandettini, P. A. Separating slow BOLD from non-BOLD baseline drifts using multi-echo fMRI. *Neuroimage* **105**, 189–197 (2015).

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